Recent changes in the spring microplankton of Lake Baikal, Russia

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ABSTRACT

Lake Baikal is facing several environmental stressors, including climate change and nearshore eutrophication. To assess recent ecological changes in Lake Baikal and provide a baseline for future comparisons, we sampled spring plankton communities from the pelagic zone of the lake in 2016 and compared these data with unpublished and published historical information going back to 1990. In 2016, one pelagic long-term monitoring station was sampled in early spring (March) during ice cover and 21 long-term monitoring stations located throughout the lake were sampled in late spring (May-June). We measured water chemistry parameters at most stations and the abundance, taxonomic composition and biomass of bacteria, ciliates and phytoplankton at several locations in different areas of the lake. Biotic parameters from 2016 were compared with historical data, showing significant changes in the spring pelagic microbial community since the 1990s. We show increased quantities of small species, mixotrophic ciliates, and the appearance (or increasing number) of small coloured and colourless fla-gellates. We also show substantially decreased densities of formerly dominant heavily silicified diatoms such as Aulacoseira spp. Since 2007, Synedra acus subsp. radians, a smaller and weakly silicified diatom, has dominated the spring plankton of the lake. These results suggest that Lake Baikal's pelagic plankton community may be changing, with climate likely playing a dominant role in these changes.

1. Introduction

Large lakes provide numerous ecosystem services to humanity, including drinking water, fisheries and recreation. However, their ability to provide these services is imperilled by a mix of often interacting anthropogenic stressors, with nutrient pollution and climate change being among the most important. For example, nutrient pollution has resulted in both localized and lake-scale alterations of primary producer community composition and abundance in such large lakes as Onega, Ladoga, Victoria and the Laurentian Great Lakes (Beeton, 1965; Chekryzheva, 2008; Petrova et al., 2010; Hampton et al., 2018), with frequently negative impacts on ecosystem services. Climate warming has also been shown to impact the ecology of large lakes, including changes to the timing, community composition and abundance of phyto- and zooplankton (e.g., Hampton et al., 2008; Rühland et al., 2008; Izmest'eva et al., 2011; Reavie et al., 2017). Understanding the nature of environmental changes and their different drivers in large lakes is essential to effective management of these important ecosystems.

Central Siberia's Lake Baikal, the world's oldest and deepest lake, contains 20% of global liquid surface freshwater and is home to thousands of endemic species, including freshwater seals and commercially important fish (Kozhov, 1963). Despite its size and relative isolation, Lake Baikal has not escaped anthropogenic-caused environmental changes. The littoral regions of the lake have recently begun displaying clear symptoms of nutrient pollution, including benthic algal blooms, declines in endemic sponge health and changes to nearshore planktonic communities with increased abundance of nutrient pollution-tolerant ciliate and phytoplankton species (Kravtsova et al., 2014; Timoshkin et al., 2016; Bondarenko and Logacheva, 2017). Lake Baikal's waters have also been warming and ice cover duration decreasing (Shimaraev and Domysheva, 2013). Warming has been linked to changes in phytoplankton and zooplankton communities in the southern area of the lake (Hampton et al., 2008; Izmest'eva et al., 2011; Katz et al., 2015) and to lake-wide changes of late-summer zooplankton communities and chlorophyll *a* concentrations (Izmest'eva et al., 2016).

In this paper, we sought to determine whether spring microplankton communities in Lake Baikal changed in recent years. Spring is an important period in Lake Baikal, historically corresponding to the time of the highest algal biomass and rates of primary production (Antipova,

1963; Votintsev et al., 1975; Bondarenko et al., 1996; Popovskaya, 2000; Straškrábová et al., 2005), and less is known about spatial patterns and temporal trends in the spring plankton of the lake than for the summer period. To address this knowledge gap, we conducted sampling at long-term monitoring stations, including one pelagic station during early spring (March) and at 21 stations throughout the lake, in late spring (May-June) of 2016. We collected water chemistry parameters from all locations and microplankton (including bacteria, ciliates and phytoplankton) from a subset of stations. We also used literature and previously-unpublished archival data to examine temporal trends in spring planktonic communities going back to 1990. Our main objectives were to determine whether the spring plankton of the lake changed in past decades, attempt to assess whether changes are likely driven by nutrient pollution or climate, and provide a baseline for future studies of the plankton of the lake.

2. Materials and methods

2.1. Study sites and sampling

The pelagic plankton of Lake Baikal were sampled during two stages of their spring development – in early spring, during the ice-cover period (March 14, 2016) and in late spring (late May- early June 2016). In March, samples were collected from the ice at one pelagic station in Southern Baikal, located 7 km from Cape Beryozovyi (N 51°47.244′ E 104°56.346′, depth 1450 m). The ice at the station was 74 cm thick with a 10 cm-thick layer of snow. A Ruttner water-sampler was used to collect water from 0, 2, 5, 10, 15, 20, 25, 50, 100, 200, 400, 600, 800, 1000, 1200, 1300, 1400 m depths. In late spring, samples were collected from aboard the research vessel "G.Yu. Vereshchagin" using an SBE-32 Carousel Water Sampler (Sea-Bird Electronics, USA) at 21 stations throughout the lake (Fig. 1). These stations were sampled on a regular basis since 1960 (Votintsev et al., 1975; Popovskaya, 1987; Bondarenko et al., 1996; Popovskaya, 2000). Water chemistry and plankton samples were taken at 0, 2, 5, 10, 15, 20, 25, and 50 m. Water temperature and transparency were measured using a CTD-profiler SBE-25 (Sea-Bird Electronics, USA) and a Secchi disk, respectively. Since some stations were sampled at dusk or at night, Secchi depths were available only for 7 stations.

2.2. Water chemistry analyses

Water for nutrient analyses was filtered on board the ship, and the filtrate refrigerated and analysed within 10 h of sampling. Soluble reactive phosphorus (SRP), nitrate, nitrite, silica and ammonium ions were analysed in water filtered through mixed cellulose ester membrane filters with 0.45 μm pore size (Advantec, Japan). Concentrations of dissolved nutrients were determined using spectrophotometric methods (spectrophotometer PE-5400VE, Ecroschem, Russia). SRP was measured by the Denigès-Atkins method in modification with tin chloride. Ammonium ions were detected by indophenol method, nitrate was measured with sodium salicylate (Boeva, 2009) and nitrite was determined with Griss reagent. Dissolved silica was determined from a yellow silicomolybdate complex (Wetzel and Likens, 2000).

For determinations of chlorophyll *a* concentration, 1 L of water was filtered through a 0.4 μm polycarbonate filter. Algal pigments were extracted with acetone (90%) overnight in the dark at 4 °C (after ultrasonic treatment). The supernatant was centrifuged and chlorophyll *a* was measured with a Cintra-2020 spectrophotometer at 664, 647 and 630 nm and calculated based on equations provided by Parsons et al. (1984).

2.3. Plankton composition analyses

Water samples were analysed to determine the abundance and biomass of bacteria, autotrophic picoplankton, ciliates and phytoplankton. Microplankton characterization was performed from the station sampled in March and from a number of stations sampled in the May-June period. Phytoplankton characterization was performed at one station from each of the southern, central and northern basins of the lake (stations 3, 9 and 15 in Fig. 1). Ciliate characterization was only performed on samples from stations 3 and 15. Bacterial abundance was determined at 10 stations.

The samples for quantitative counting of autotrophic picoplankton and bacteria were fixed with 2% formaldehyde and filtered through 0.22-mm pore-size polycarbonate filters (Millipore). The filters for bacteria counting were stained with 4′,6-diamidino-2-phenylindole, dihydrochloride (DAPI) solution (Porter and Feig, 1980). Filters were air-dried and placed on a drop of non-fluorescing immersion oil. Ready preparations were stored in darkness at 4 °C. Filters were examined using Axio Imager.M1 microscope (Carl Zeiss, Germany), equipped with
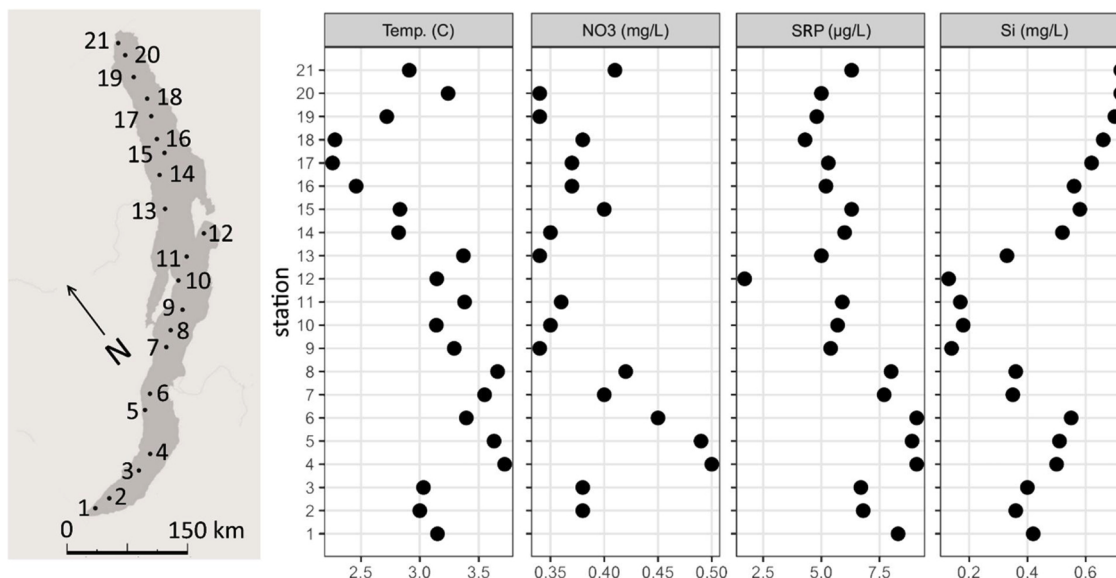

Fig. 1. Map of sampling sites and spatial variation of surface temperature and nutrient concentrations in the top 0–50 m depth in Lake Baikal in late May and early June of 2016.
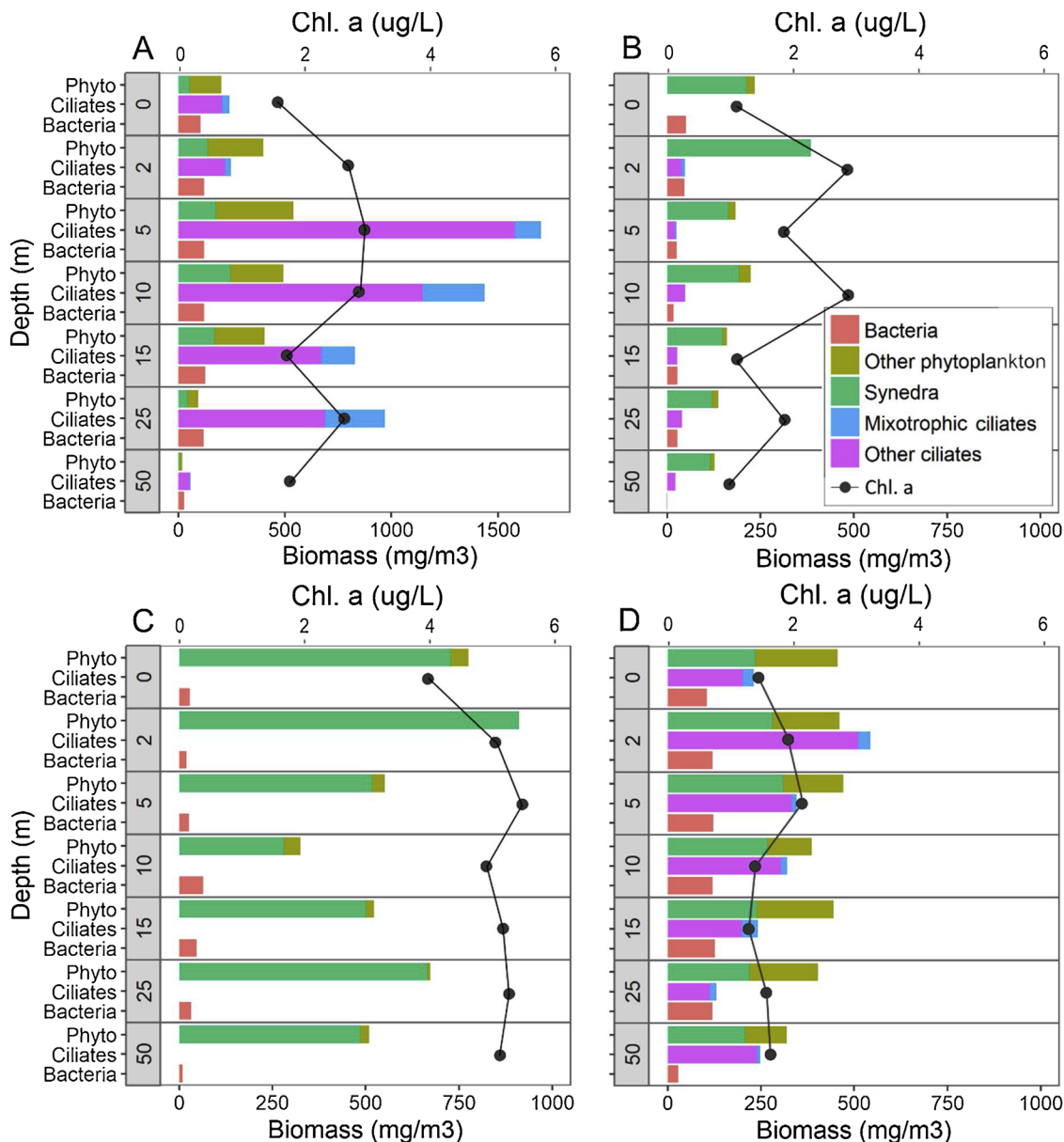
Fig. 2. The depth distribution of biomass of microplankton and chlorophyll *a* in early and late spring of 2016: A) Southern Baikal under ice (March 14, 2016), B) Southern Baikal (station 3) in late spring (May 27, 2016), C) Central Baikal (station 9) in late spring (May 30, 2016) and D) Northern Baikal (station 15) in late spring (June 1, 2016). Note that ciliates were not counted at the central Baikal station.

a HBO 100 W mercury lamp and AxioCam MRm and MRc5 cameras. Registration was done by means of oil lens x100 (Plan-Fluar). Two filter sets were used: UV excitation for DAPI-stained bacteria; green excitation for picoplanktonic cyanobacteria with orange-red fluoresce due to the presence of phycobilins. Cells were counted from 30 view fields with subsequent averaging. Total number of the cells registered on a filter was 300-500 as described previously (Belykh and Sorokovikova, 2003).

Samples (1 L volume) for identification of phytoplankton and ciliates were fixed by Lugol's solution and then concentrated by sedimentation. Algae were counted twice in a 0.1 mL Nageotte chamber under a "Peraval" light microscope with ×720 and ×1200 magnification. Algal biomass was calculated from algal numbers using individual cell volumes. To determine the biovolume, 100–200 cells of each species were measured. Algae were identified according to (Matvienko and Litvinenko, 1977; Starmach, 1985; Tsarenko, 1990; Gleser et al., 1992). Because thin cells of *Synedra acus* subsp. *radians* (Kütz.) Skabitchevsky formed by the sexual process did not have silica valves, 50 mL samples

were filtered onto 1 μm pore-size "Millipore" polycarbonate filters and stained by DAPI for visualisation of nuclei and chloroplasts. Then the cells were counted directly on the filter using an Axio Imager.M1 microscope with ×200 magnification. Ciliates were counted in triplicate in a 0.1 mL Nageotte chamber under a Peraval microscope (Zeiss, Germany) with ×200 magnification. Ciliate cell volumes and their individual masses were calculated by the method of Foissner et al. (1994). The biomass of ciliate algosymbionts was calculated assuming they constitute 75% of the host-cell based on estimates for *Limnostrombidium* by Hecky and Kling (1981).

To compare the plankton from spring 2016 to earlier years, we used published data (Votintsev et al., 1975; Popovskaya, 1987; Bondarenko et al., 1996; Belykh and Sorokovikova, 2003) and materials from the archives of the authors of the article, obtained by similar methods. Historical data included information on the abundance and biomass of early and late spring microplankton in Southern Baikal going back to 1990.

Table 1

Average abundance (cells/L ± standard error) of common phytoplankton species (more than 5% abundance at any stations) in the 0-50 m layer in Lake Baikal in March and May - June 2016.

	South Baikal, March 14	South Baikal, Station 3 May 27	Central Baikal, Station 9 May 30	North Baikal, Station 15 June 1
BACILLARIOPHYTA				
Aulacoseira baicalensis (K. Meyer) Simonsen	0	0	0	5391 ± 1490
A. islandica (O. Müll.) Simonsen	6 ± 1	541 ± 325	192 ± 147	373 ± 301
Cyclotella minuta Antipova	236 ± 152	69 ± 43	38 ± 4	78 ± 8
Nitzschia graciliformis Lange-Bertalot *et* Simonsen emend Genkal et Popovskaya	1836 ± 661	1324 ± 445	36 ± 4	188 ± 165
Stephanodiscus meyeri Genkal et Popovskaya	190 ± 146	1126 ± 552	41 ± 5	230 ± 31
Synedra acus subsp. *radians* (Kütz.) Skabitsch.	120280 ± 53105	103465 ± 18718	475453 ± 45026	137827 ± 81934
Asterionella formosa var. *formosa* Hass.	38 ± 5	0	0	0
CHLOROPTYTA				
Chlamydomonas komma Pascher	3358 ± 2304	315 ± 48	0	207 ± 96
Koliella longiseta (Vischer) Hindák	111956 ± 56418	21581 ± 1938	75988 ± 14080	7949 ± 2280
Elakatothrix genevensis (Reverdin) Hindák	76 ± 21	63 ± 6	0	0
CHRYSOPHYTA				
Chrysospaerella baicalensis Popovskaya	scales	scales	scales	scales
Dinobryon cylindricum Imhof	6167 ± 4974	922 ± 190	2255 ± 887	24137 ± 7688
D. sociale Ehrenberg	56 ± 9	365 ± 188	50 ± 5	17179 ± 4376
Kephyrion sp.	0	29 ± 11	50 ± 5	0
HAPTOPHYTA				
Chrysochromulina parva Lackey	437 ± 156	0	0	256 ± 123
CRYPTOPHYTA				
Cryptomonas reflexa (Marsson) Skuja	1024	0	0	572 ± 271
C. erosa Ehrenberg	193	0	0	31 ± 5
C. ovata Ehrenberg	142	0	0	0
Rhodomonas pusilla (Bachm.) Javorn.	12514 ± 5614	2170 ± 468	2653 ± 572	2588 ± 469
DINOPHYTA				
Glenodinium sp.	109 ± 72	1216 ± 307	1207 ± 555	1401 ± 912
Gymnodinium baicalense var. *minor* Antipova	1894 ± 1186	38 ± 16	0	0
Gyrodinium helveticum (Penard) Y. Takano et T. Horiguchi	2309 ± 1551	862 ± 258	326 ± 226	617 ± 234
Peridinium baicalense Kiselev et Cvetkov	113 ± 76	269 ± 103	144 ± 96	231 ± 32

3. Results

3.1. Water temperature and chemistry

In 2016, the ice-cover season in the southern basin of Lake Baikal ended around April 20 and approximately a month later in the northern part of the lake. During the under-ice period (in March), the water column at the ice-sampling station was inversely stratified, with surface water temperate of 0.45 °C. Secchi depth was 10.5 m. Concentrations of soluble reactive phosphorus (SRP), nitrogen and silica in the surface water (0–25 m) were low and gradually increased with depth. SRP in the top 50 m layer was equal to 0.0065 mg/L, nitrate 0.4 mg/L, ammonia 0.0037 mg/L and silica 0.44 mg/L. Concentrations of SRP, nitrate, ammonia and silica averaged 0.012, 0.58, 0.004 and 1.17 mg/L, respectively, at depths below 100 m. In late spring, water temperature and chemistry varied between stations (Fig. 1). Surface water temperatures (0 m) were generally higher in the central basin (3.43 °C, ± 0.20 SD) than in the southern (3.23 °C, ± 0.33 SD) and northern basins (2.77 °C, ± 0.38 SD). Most stations in southern and central areas of Lake Baikal were isothermal, while stations in Northern Baikal exhibited inverse stratification, probably because of more recent ice-off there. Secchi depth was measured at 7 stations and averaged 12.1 m (± 6.25 SD). Across all stations, nitrate, SRP and silica concentrations in the surface water (0–50 m) averaged 0.39 mg/L (± 0.05 SD), 0.006 mg/L (± 0.0018 SD) and 0.45 mg/L (± 0.19 SD), respectively. Concentrations of nitrate and SRP in surface waters were on average higher in the southern basin of the lake than in Central and Northern Baikal (Fig. 1). Conversely, silica concentrations were the highest in Northern Baikal and lowest in the central basin (Fig. 1).

3.2. Chlorophyll a concentrations

In early spring, chlorophyll *a* concentrations under the ice ranged from 1.58 to 2.79 μg/L in the upper 0–50 m layer (Fig. 2), with an average of 2.21 μg/L. At 100 m, chlorophyll *a* concentration was only 0.15 μg/L. In May-June, surface (0–50 m) chlorophyll *a* concentrations at seven pelagic stations averaged 2.25 μg/L and varied between 0.64 μg/L at station 6 (Krasny Yar Cape –Selenga River) and 4.97 μg/L at station 9 (Ukhan Cape – Tonky Cape), where a *S. acus* bloom was occurring. The highest chlorophyll *a* concentrations were measured in Barguzin Bay (station 12) (11.9 μg/L) and near the mouth of the Barguzin River (12.1 μg/L).

3.3. Microplankton

3.3.1. Bacterioplankton

Average bacterioplankton densities and biomass in the southern basin (the top 25 m) were 1,759,000 cells/mL and 121 mg/m³ under the ice. In late spring, density and biomass in the southern basin was lower (449,000 cells/mL and 31 mg/m³). In the central basin in late spring, average densities were 540,000 cells/mL (Station 9: Ukhan Cape – Tonky Cape) and 876,000 cells/mL at station 6 (Krasny Yar Cape – Selenga River). In the northern basin, bacterioplankton densities varied from the minimum values 444,000 cells/mL at station 15 (Cape Elokhin − Davsha village) to the maximum values 2,027,000 cells/mL at station 20 (Tya River – Nemnyanka Cape). At all sampling locations, bacteria were approximately evenly distributed in the top 25 m, but their numbers decreased sharply at 50 m depths (Fig. 2).

3.3.2. Picoplanktonic cyanobacteria

In March, picoplanktonic cyanobacteria (PCB) were uniformly distributed in the upper 0–25 m layer at average density and biomass of 33,000 cells/mL and 18 mg/m^3. PCB were most abundant directly under the ice (42,000 cells/mL) and sharply decreased at a depth of 50 m and lower. PCB comprised 2% in number and 15% in biomass of the total bacterioplankton within the 0–25 m layer and 4.8% of the total biomass of autotrophs. *Cyanobium* and *Synechococcus* dominated total numbers; the endemic *Synechocystis limnetica* contributed only 5% to the total number of PCB in the 0–25 m layer.

3.3.3. Phytoplankton

Despite the patchy snow cover on the ice, phytoplankton bloomed intensively in March (Fig. 2, Table 1). The total phytoplankton biomass gradually increased from 202 mg/m^3 at the surface to a peak of 540 mg/m^3 at 5 m, then gradually decreased at 15 m to low and then negligible values at 25 m and 50 m (Fig. 2). The diatom *S. acus* and the chlorophyte *Koliella longiseta* dominated total phytoplankton numbers, each making up 45% and 42% (respectively) of total algal abundance in the 0–50 m layer. Cryptophytes were also present, contributing 2 to 7% of densities. The depth distribution varied between taxonomic groups. Diatoms were most abundant in the 10–50 m layer, while green algae concentrated under the ice and the top 10 m of the water column. Cryptophytes were most abundant at depths from 15 to 50 m while chrysophytes and dinoflagellates were uniformly distributed in the 0–50 m layer. Immediately under the ice and at the 2 m depth, we observed *Chlamydomonas* (3,000–10,000 cells/L) and *Chrysochromulina* (2500 cells/L), as well as nanoplanktonic colourless flagellates (cells 5–6 μm wide and 10–12 μm long, possibly *Telonema*) not previously described from Lake Baikal.

In late May, the average biomass (227 mg/m^3) and abundance (151,000 cells/L) of phytoplankton in Southern Baikal was lower than in March in the 0–25 m layer. Late spring phytoplankton abundance and biomass was on average higher in the middle (518,000 cells/L, 607 mg/m^3) and northern basins (209,000 cells/L, 438 mg/m^3). Algal biomass was more evenly distributed in the top 50 m of the water column in late spring than in March (Fig. 2). The phytoplankton composition in the middle and southern basins resembled that of March and was dominated by *S. acus* and *K. longiseta*. At that time, 70% of the *S. acus* were composed of thin cells formed by sexual reproduction without visible silicified cell walls. Diatoms create their frustules under dissolved silica concentrations higher 0.2 mg/L (Wetzel and Likens, 2000) but the concentration of silica in May in the middle of the lake was minimal, 0.14 ± 0.21 mg/L.

Northern Baikal was richer than the middle basin in number of species, but phytoplankton biomass was lower, 319-461 mg/m^3 (Fig. 2). Besides *S. acus* numbering 35,000-417,000 cells/L, the dominant species consisted of *Dinobryon sociale* and *D. cylindricum*, together adding up to 50,000 cells/L. The diatom *Aulacoseira baicalensis*, which typically dominated spring phytoplankton in Lake Baikal in the 20th century, was recorded in unusually low densities, 2,000–7,000 cells/L.

3.3.4. Ciliates

Plankton in March contained 28 species of ciliates (Table 2) and was abundant in oligotrichs, including two Baikalian species *Tintinnidium gajewskajae* and *Tintinnopsis* sp. Except these two tintinnids, two other species *Histiobalantium* (*Sulcigera*) *comosa* and *Liliimorpha viridis* belonging to the complex of large endemic Baikal ciliates were observed in small numbers.

In early spring, oligotrichs contributed 86.0% to total ciliate number and 60.7% to ciliate biomass in the 0–50 m layer. Their composition and abundance differed along the water column. In the upper under-ice waters, small (< 40 μm) oligotrichs *Rimostrombidium* spp. prevailed but deeper they were gradually replaced by *Limnostrombidium viride* and *Strombidium gracile* and by tintinnids. Maximal number of the oligotrichs, 35,000 cells/L, and total number of ciliates, 40,000 cells/L, were

obtained at depths between 5 and 10 m. *H. comosa, Askenasia* spp. and *Mesodinium* cf. *pulex* also increased their numbers at these depths, while the mixotrophic *Liliimorpha viridis* was uniformly distributed in the 0–25 m layer. The total number and biomass of the ciliates were high up to a depth of 25 m but decreased sharply at 50 m (Fig. 2). The number of the mixotrophic ciliates in spring plankton was unusually high. Biomass values of their algosymbionts, 122.0–289.5 mg/m^3, were comparable to the phytoplankton biomass and comprised half of the total biomass of autotrophs, 49.3% in the 0–25 m layer and 53.0% in the 0–50 m layer. The main species containing algosymbionts was *Limnostrombidium viride* dominating at that time.

In late May, the number of ciliate species in the 0–50 m layer of Southern Baikal decreased to about half of that in March. The two oligotrichs *Strombidium gracile* and *Tintinnopsis* sp. dominated in numbers while *H. comosa* was subdominant. The mixotroph *L. viride*, which was abundant in March, was rare. The abundance of ciliates in the 0–50 m layer was lower than in March (500–600 cells/L, the total biomass to 22–48 mg/m^3), and their vertical distribution was uniform. In early June, the pelagic zone of Northern Baikal was inhabited by 15 ciliate species, whose specific composition differed from that in Southern Baikal. *H. comosa* dominated the Northern Baikal ciliates, and its number exceeded the number of other ciliates by several times; its biomass comprised more than half of total ciliate biomass. The oligotrichs *L. viride* and *S. gracile* were subdominant while other species usually dominant in high-productivity years, namely *Marituja pelagica*, *Liliimorpha viridis*, *Tintinnidium gajewskajae*, and *Tintinnopsis* spp., were observed in small numbers. The total number and biomass of the ciliates in the 0–50 m layer were higher than in late May in Southern Baikal but lower than in March, i.e. 1778 to 5843 cells/L and 130 to 543 mg/m^3.

3.4. Long term context and change

Plankton biomass data from Southern Baikal in 2016 was compared to early and late spring data from Southern Baikal collected between 1999 and 2007 (Fig. 3). Total plankton biomass in early spring (under ice) was higher and more variable than late spring (open water) biomass throughout all years (760.5 ± 742.9 SD vs 290.6 ± 72.9 SD mg/m^3). In 2016, early spring biomass (1459 mg/m^3) was higher than the average for the season. Plankton biomass in late spring in 2016 (303 mg/m^3) was comparable to that observed in other 4 years for which data are available. In terms of relative community composition, the largest difference between early and late spring is larger (and more inter-annually variable) contribution of ciliates to total biomass under ice compared to late spring (34.9 ± 16.7 SD vs 13.5 ± 3.7 SD%). Ciliates comprised a larger fraction of total biomass in early spring of 2016 than average (65.5%). In late spring, the relative contribution of different groups to total biomass in 2016 was lower than that of bacteria and higher contribution of phytoplankton than in the other 4 years.

Long term data from 1990 to 2016 show a significant increase in the density of the diatom *S. acus* (linear regression, square-root transformed concentrations to approximate regression assumptions, $R^2 = 0.26$, $p = 0.0044$) in the southern basin of Lake Baikal during late spring (Fig. 4A). Concomitantly, there was a significant and sharp decrease in the densities of *Aulacoseira* spp. (linear regression, $\log_{10}$ transformed concentrations to approximate regression assumptions, $R^2 = 0.60$, $p < 0.0001$) with very low numbers after 2007 (Fig. 4B). There has been no linear trend in ice cover duration in the southern basin of the lake between 1990 and 2016, and neither *S. acus* nor *Aulacoseira* spp. concentrations were significantly related to ice cover duration (Fig. 4C, D).

4. Discussion

In connection with recent changes in the ecosystem of Lake Baikal,

Table 2

Average abundance (cells/L ± standard error) of ciliate species in the 0–50 m layer in Lake Baikal in March and May-June 2016.

	South Baikal, March 14	South Baikal, Station 3 May 27	North Baikal, Station 15 June 1
HAPTORIA			
Askenasia cf. *acrostomia* Krainer et Foissner, 1990	75 ± 29	0	0
Askenasia cf. *chrolelligera* Krainer et Foissner, 1990	99 ± 26	0	0
Askenasia volvox (Eichwald, 1852) Kahl, 1930	90 ± 46	0	43 ± 21
Cyclotrichium brunneum Gajewskaja, 1933	19 ± 18	0	0
Cyclotrichium sp.	10 ± 8	0	0
Didinium chlorelligerum Kahl, 1935	57 ± 51	0	0
Liliimorpha viridis Gajewskaja, 1928	194 ± 39	8 ± 7	109 ± 22
Mesodinium pulex (Claparede et Lachmann, 1859) Stein, 1867	149 ± 57	0	75 ± 35
OLIGOHYMENOPHOREA			
Histiobalantium comosa (Gajewskaja, 1928) Antipa et al., 2016	1236 ± 263	85 ± 25	1554 ± 264
Marituja pelagica Gajewskaja, 1928	0	9 ± 7	104 ± 46
OLIGOTRICHEA			
Limnostrombidium pelagicum (Kahl, 1932) Krainer, 1995	264 ± 128	0	0
Limnostrombidium viride (Stein, 1867) Krainer, 1995	5707 ± 1998	16 ± 14	400 ± 140
Rimostrombidium humile (Penard, 1922) Petz et Foissner, 1992	622 ± 112	0	0
Rimostromdium cf. *hyalinum* (Mirabdullaev, 1985) Petz et Foissner, 1992	1130 ± 73	0	0
Rimostromdium inopinatum Potapskaya, Obolkina, 2012	865 ± 111	8 ± 7	61 ± 37
Rimostrombidium cf. *vicinum* Potapskaya, Obolkina, 2012	13 ± 11	8 ± 7	0
Strombidium gracile (Potapskaya, 2012) Obolkina, 2015	2916 ± 1502	92 ± 34	341 ± 67
Strombidium crassum (Potapskaya, 2012) Obolkina, 2015	126 ± 111	0	125 ± 46
Strobilidium sp. nov.	43 ± 17	8 ± 7	0
Tintinnopsis sp. 1 (*T. davidoffi* var. *cylindrica* Daday f. *minima* Gajewskaja, 1933)	2789 ± 772	153 ± 35	203 ± 29
Tintinnopsis sp. 2	50 ± 20	15 ± 14	26 ± 16
Tintinnidium gajewskajae (*T. fluviatile* f. *cylindrica* Gajewskaja, 1933) Obolkina, 2015	2319 ± 851	16 ± 15	209 ± 109
PROSTAMATEA			
Longifragma obliqua (Kahl, 1926) Foissner 1984	24 ± 2	0	0
Urotricha intermedia Obolkina, 2015	0	0	44 ± 22
Urotricha vernalis Obolkina, 2015	73 ± 70	0	0
Urotricha sp. 1 (d = 30-40 μm)	70 ± 36	0	0
Urotricha sp. 2 (d = 50-60 μm)	245 ± 130	6 ± 5	8 ± 7
PHYLLOPHARYNGEA			
Gajewskajophrya melosirae (Gajewskaja, 1933) Matthes, 1988	20 ± 18	0	0
Staurophrya elegans Zacharias, 1893	12 ± 11	0	0
Unknown ciliates, 80-100 μm	103 ± 30	14 ± 8	76 ± 42

the state of the lake's pelagic microplankton was evaluated in the spring of 2016. The short life cycle and high reproductive rates of microplankton mean that this community may respond rapidly to environmental changes and help detect shifts in the ecosystem. We sought to assess the community of the microplankton in order to provide a baseline for future studies and to compare our results with historical data from the lake.

4.1. Nutrients

The study was performed during two stages of spring plankton development – in early spring, during the ice-cover period (March 2016) and in late spring (late May-early June 2016). The spring phytoplankton in Lake Baikal begin to develop under the ice, and this under-ice bloom is accompanied by a decrease in nutrients in the upper water layer (0–50 m). Previous research showed maximum concentrations of nutrients in the surface waters in December-February (nitrate – 0.086-0.089 mg/L, phosphate – 0.007-0.008 mg/L, silica – 1.22–1.9 mg/L; Votintsev et al., 1975). During years with mass development of diatoms under ice, the concentration of nutrients was significantly reduced: nitrogen was below detection, the phosphate content reached 0.002-0.003 mg/L and silica – 0.75–1.31 mg/L (Votintsev et al., 1975). Most nutrients and organic substances (60–90%) enter the lake with river waters, with maximum inputs between May and October during periods of higher water flows (Sorokovikova et al., 2010). The largest tributaries of Lake Baikal – Selenga, Barguzin, Upper Angara, and Turka – contribute up to 90% of nutrients to the lake. The greatest inflow of nutrients and organic substances occurs in the central part of the lake through the Selenga, Barguzin, and Turka rivers.

May through early June is the period of ice breakup on the lake. It starts in the southern basin in early May and slowly moves northward. The ice breakup begins first near the western shore, then – near the eastern one. This time can be regarded as the onset of the spring isothermal conditions, which last approximately one month (Votintsev et al., 1975). After ice breakup, the upper water layer is enriched with nutrients due to their supply from the deep water layers and as result of regeneration during the decomposition of dead plankton.

High spatial heterogeneity was detected in the distribution of nutrients within the lake in late spring of 2016. The nitrogen content was higher than the values observed in the 1970s; NO_3 values ranged within 0.32-0.50 mg/L (our data) compared to 0.23-0.29 mg/L (Votintsev et al., 1975). Our values were also higher than average NO_3 values measured in the three basins in late spring 2007–2011 (0.39 vs. 0.29 mg/L, Popovskaya et al., 2015). SRP concertation was 0.0062 mg/L, and was very similar to that observed in the 1970s (Votintsev et al., 1975) and in 2007–2011; (Popovskaya et al., 2015). In contrast, the silica content (0.3-0.59 mg/L) was significantly lower than in the 1970s (0.95–1.05 mg/L), and somewhat lower the late spring lake-wide average in 2007–2011 (0.63 mg/L, Popovskaya et al., 2015). Higher concentrations of nitrate and SRP were observed at stations under the influence of rivers, especially the Selenga River. The nitrate content was the lowest in the central basin of the lake. The distribution of silica depended on the development of diatoms in plankton. High production of *Synedra* in the southern and central basins (92–97% from total biomass phytoplankton) was accompanied by low concentrations of silica, whereas high concentrations of silica in the north of the lake were likely due to lower diatom production there (60% from total phytoplankton biomass).
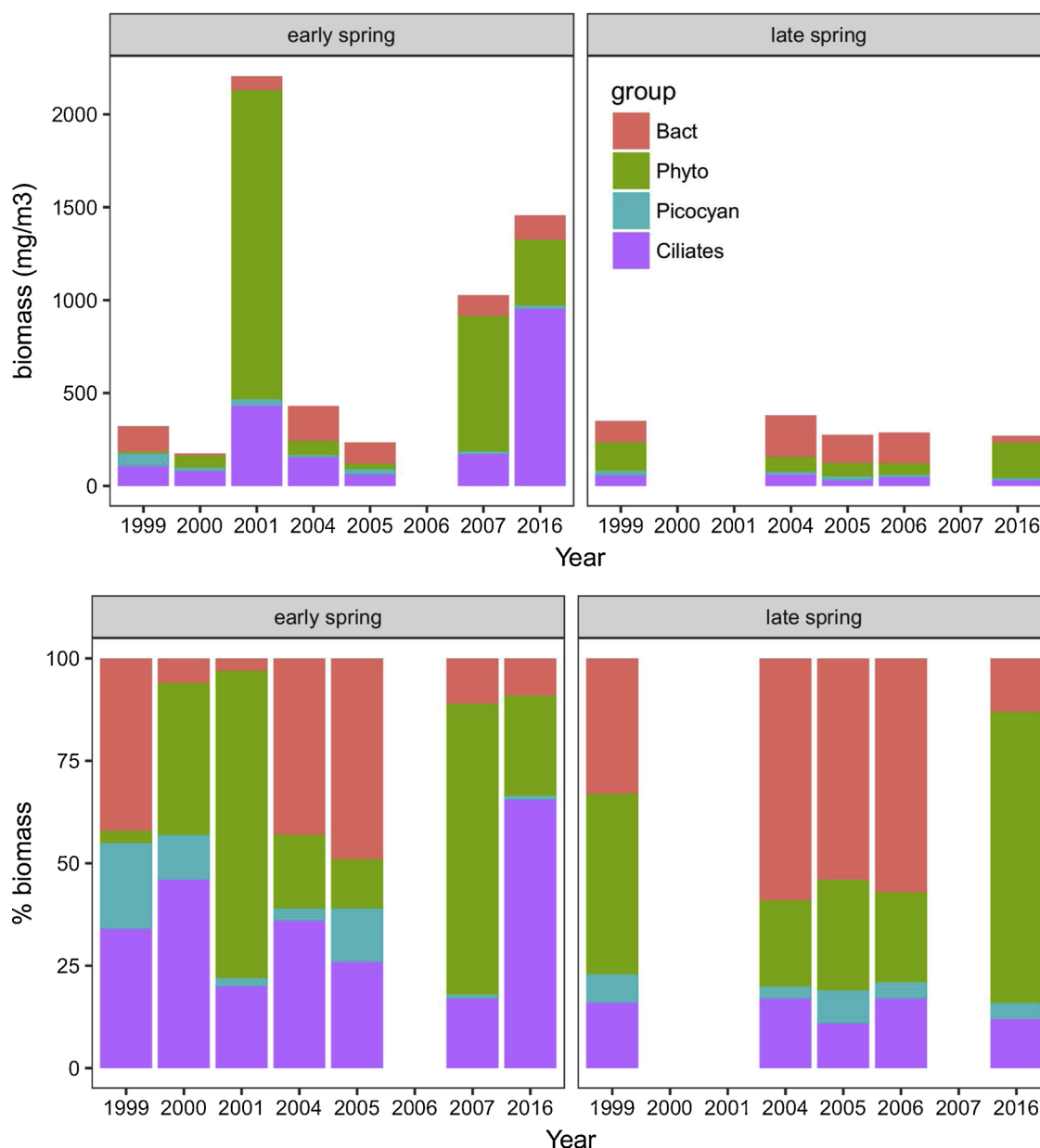
Fig. 3. Time series of total and relative microplankton biomass in Southern Baikal in early spring (under ice, March) and late spring (May-June).

4.2. Planktonic communities

The total biomass and taxonomic composition of microplankton in the pelagic zone of Southern Baikal differed between the beginning and end of spring (Fig. 2). For example, the total microplankton biomass in the 0–25 m layer equalled 1459 mg/m^3 in mid-March under the ice and decreased almost 5-fold to 303 mg/m^3 in late May. During the ice-cover period, flagellates and floating bundles (agglomerates) of green algae were observed directly under the ice. Poorly silicified *Synedra* and ciliates were evenly distributed in the upper water layer (0–25 m). Such a pattern of plankton distribution was due to inverse stratification, with under-ice convective mixing maintaining cells in suspension in the upper ~25 m of the water column. The high chlorophyll *a* content in the 2016 spring plankton was mostly due to high densities of mixotrophic ciliates, as revealed by high correlation coefficients between water chlorophyll *a* content and the biomass of algosymbiont ciliates (r = 0.89 at p < 0.05) and the total autotrophic biomass (phytoplankton and algosymbionts) with r = 0.80. Mixotrophs possess some advantages in competition for food in comparison with other consumers

of autotrophs and bacteria under oligotrophic conditions (Foissner et al., 1999). Thus, their appearance may indicate a food deficit, particularly phytoplankton biomass decrease (Beaver and Crisman, 1989; Pace et al., 1990; Mitra, 2013; Ptacnik et al., 2016). An additional factor promoting their abundant development might be light (Ptacnik et al., 2016). Thus, the dominance of the mixotrophic *L. viride* in the under-ice plankton may have been facilitated by the abundance of small algae and bacteria and sufficient light conditions under the ice because of the patchy nature of snow cover on the ice.

In late May, there were differences in the abundance and composition of microplankton at the southern, central and northern Baikal stations. The lower biomass of plankton in Southern Baikal is likely explained by the onset of isothermal conditions and deep mixing causing plankton to become distributed through a thicker layer of water. Late spring phytoplankton biomass and abundance were on average higher in the central (518,000 cells/L, 607 mg/m^3) basin where isothermal conditions only began to appear. The species composition in Northern Baikal was richer than in the central basin but phytoplankton biomass was lower there, a typical situation for the lake (Bondarenko
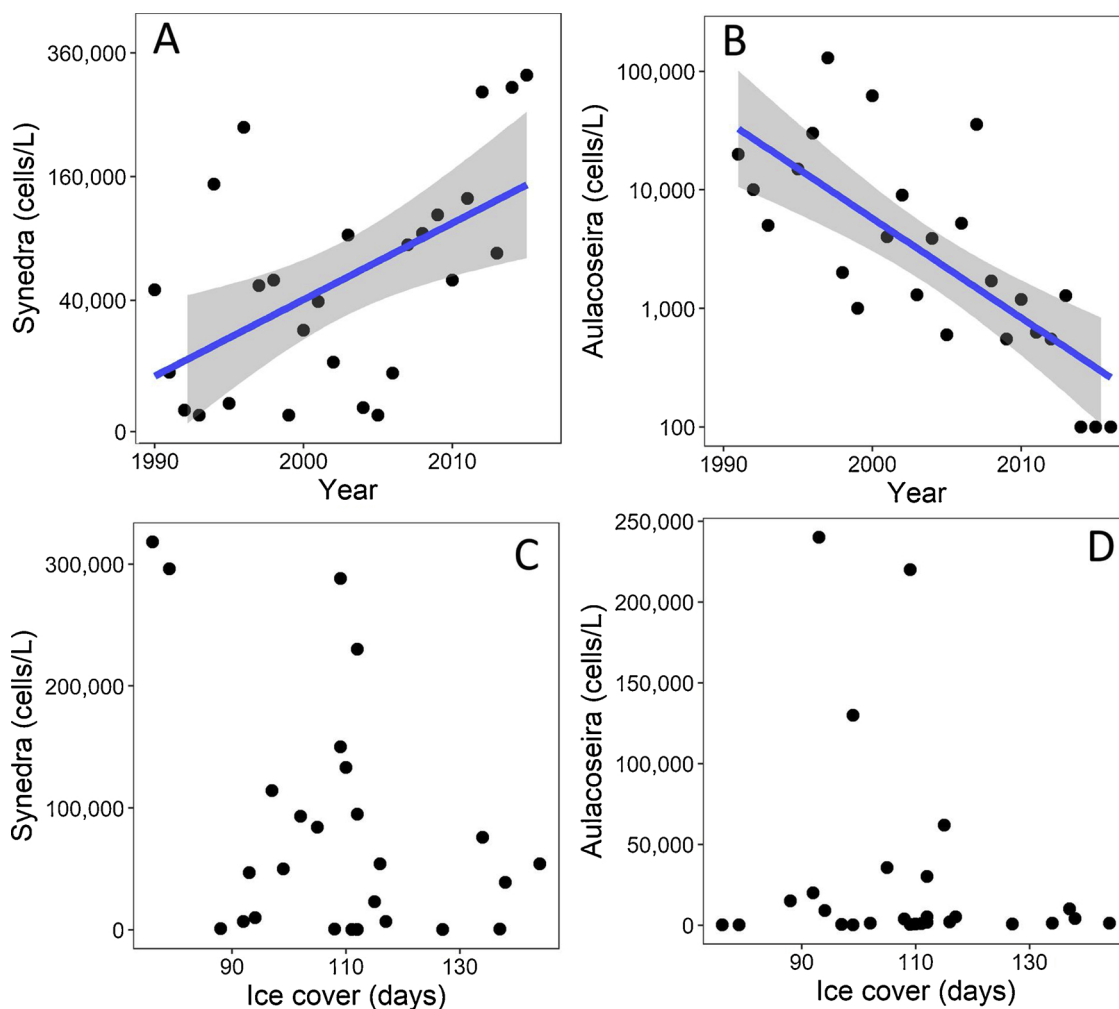
Fig. 4. Trends in abundance of *Synedra acus* (A) and *Aulacoseira* spp. (B) in the top 50 m layer in Southern Baikal between 1990 and 2016. Linear regression lines (with standard error) for square-root transformed densities of *Synedra acus* and log-transformed *Aulacoseira* spp. vs. year are shown (note transformed axes). Untransformed spring *Synedra* (C) and *Aulacoseira* (D) abundance relative to ice cover duration over the preceding winter.

et al., 1996; Popovskaya et al., 2015).

4.3. Temporal changes in microplankton biomass

Spring algal biomass in Lake Baikal varies very significantly from year to year – from 500 mg/m^3 or less in low-productivity years to more than 1 g/m^3 in high-productivity years (Antipova, 1963; Kozhov, 1963; Popovskaya, 1987, 2000; Bondarenko et al., 1996; Katz et al., 2015; Popovskaya et al., 2015). In the high-productivity years, historically called "Melosira years", large-celled diatoms of the genus *Aulacoseira* (*A. baicalensis* and *A. islandica*; Jewson et al., 2008; Jewson and Granin, 2015), dinoflagellates and large-celled ciliates proliferate in the plankton. In low-productivity years, the main planktonic primary contributors are nanoplanktonic cryptophytes and chrysophytes.

In recent years, the structure of spring phytoplankton appears to be changing, although continuing data collection is needed to confirm these trends. Approximately since 2007, the diatom *S. acus* has dominated the plankton at densities of 100,000–400,000 cells/L (Fig. 4). In the 1950–2000 s, *S. acus* achieved such high densities only in two successive years – in a "high-productivity year" and the next one (1958–1959 and 1982–1983, Antipova, 1963; Popovskaya, 1987). Structural changes were also recorded in the general plankton structure, i.e., small-sized species (e.g. *Chrysochromulina parva*) increased their number and new representatives of flagellates (green algae *Chlamydomonas* spp.) were observed, suggesting increased nutrient levels

(e.g., Trifonova, 1990; Wehr and Sheath, 2003; Barinova et al., 2006; Chekryzheva, 2008).

On the other hand, the typical Baikal algae *Aulacoseira baicalensis*, *A. islandica*, and *Stephanodiscus meyeri* decreased their former dominant numbers (Fig. 4; Bondarenko et al., 2017 in press). For example, in 2016, the number of *A. baicalensis* was 2,000–7,000 cells/L in Northern Baikal, and it was almost not recorded in the other two basins. As *Synedra* cells are smaller than cells of *Aulacoseira* species (1800 μm^3 in vs. 4,000–20,000 μm^3 in volume), the current spring phytoplankton biomass are lower than in previous high-productivity years: 400–900 mg/m^3 compared to 1–4 g/m^3 in the past (Antipova, 1963; Popovskaya, 1987, 2000).

Since phytoplankton, as the main food source, govern the planktonic ciliate development in Lake Baikal, the composition and abundance of ciliates varies significantly with phytoplankton productivity (Obolkina et al., 2012). Recently, small-sized ciliates became dominant in the spring plankton. This set of year-round active ciliates was typical of low-productivity phytoplankton years but now they developed along with 2–3 species from the Baikal species complex previously observed only in high-productivity years. In the previous century, Baikal ciliates were dominated by psychrophilic large species, including *Marituja pelagica*, *Histiobalantium comosa*, *Liliimorpha viridis*, *Cyclotrichium brunneum*, *Tintinnidium gajewskajae*, and *Tintinnopsis* spp., which dominated in the phytoplankton-productive years. Oligotrichs (*Strombidium gracile* and *Limnostrombidium viride*) and species from the Baikal psychrophilic

complex (*Histiobalantium comosa*, *Tintinnidium gajewskajae*, and *Tintin-nopsis* spp.) prevailed in unproductive years and other species of the Baikal complex were rare. However, in 2016, the species composition of ciliates was similar to that of the unproductive years, but their quantitative indicators exceeded those in the highly productive years by an order of magnitude, a situation which was not observed at Lake Baikal in the past. Although a composition of spring ciliates in 2016 was similar to that in the previous years, their high number and dominance of mixotroph representatives were unusual.

Ciliates made up more than 65.3% in the March plankton biomass in 2016, while phytoplankton contributed 25.1%, bacterioplankton 8.1%, and the share of autotrophic picoplankton was negligible near 1.2%. Earlier, the main contributors to biomass were bacterioplankton in the low-productivity years and phytoplankton in the high-productivity years (Obolkina et al., 2012). Based on the data for 1999–2001 and 2005–2007, the phytoplankton contributions reached about 70–80% of the total spring biomass of protists and prokaryotes in the high-productivity years and did not exceed 35% in the low-productivity years. Bacterioplankton contributed 50–60% or sometimes (for example, late spring 2004–2006) more (Sekino et al., 2007; Obolkina et al., 2012). A situation when the ciliate biomass exceeds the potential food biomass (bacterioplankton + autotrophic picoplankton + phytoplankton) by ~2 times has not been observed in Baikal spring microplankton before.

Unlike phytoplankton and ciliates, there were no obvious long-term trends in the abundance of bacterioplankton. High total numbers of bacteria observed under the ice were similar to the earlier values obtained by the dye DAPI (Straškrábová et al., 2005), slightly exceeded the average value for 1999–2008 (unpublished data of Belykh O.I.), obtained by the same method and was ~3-fold higher than the average value for 1969–1983 using erythrosine staining (Maximova and Maximov, 1989). It is established that the bacterioplankton development depends on dissolved organic substances (DOS) which may be of both terrestrial and autochthonous origin (Cole et al., 2006). Increases in primary production under the ice promote the rise of heterotrophic bacteria abundance. The elevated bacterial number under the ice was likely supported by polysaccharides secreted by phytoplankton growing under the ice (Bondarenko et al., 2012). Moreover, an additional source for growth of bacteria was ammonium present in the upper 0–25 m layer as a result of algal decomposition.

Total bacterial numbers for May and June 2016 detected in Southern Baikal were near the average multi-year value for this part of the lake (Maximova and Maximov, 1989). In the pelagic zone of the central part of the lake (station 6) and northern part (stations 19, 20), in Barguzin Bay, Maloye More Strait, and Olkhonskie Vorota Strait the abundance was higher (by 5 times) and similar to the early data obtained by the DAPI-staining method (Butina et al., 2010).

The reasons for the above-described changes in the microplankton community of the pelagic Lake Baikal are unclear. Although nitrate concentrations measured by us were higher than those in the 1970s, there were no abrupt changes in the nutrient load of the Baikal waters compared to the data obtained in the 1950s and 1960s, which serve as reference data for further studies (Popovskaya et al., 2015; Khodzher et al., 2017).

Recently observed changes in the littoral plankton of Lake Baikal are likely caused by nutrient pollution (Bondarenko and Logacheva, 2017). However, the changes in the pelagic zone (especially the disappearance of *Aulacoseira* and its replacement by *Synedra*) are probably more closely related to change in climate. While we have not found a direct relationship between ice cover duration and *Aulacoseira* or *Synedra* densities, other studies have shown that *Aulacoseira* development in Baikal depends on the timing, duration and quality of the ice cover (Shimaraev, 1971; Mackay et al., 2006; Katz et al., 2015) and that *Synedra* may be more abundant under conditions of shorter ice duration (Mackay et al., 2006). Bondarenko et al. (2006, 2012) have observed that *Aulacoseira* can attach to the bottom of the ice in both the nearshore and the offshore areas of the lake. Based on these observations,

Bondarenko et al. (2006, 2012) speculated that the success of *Aulacoseira* depends less on the total duration than the timing of the ice cover, with early ice formation being important for this alga because heavy filaments of *Aulacoseira* that are resuspended in the autumn would rapidly sink out of the plankton unless they are able to attach to the bottom of the forming ice; these ice-attached cells then serve as the "inoculum" for the spring bloom. Similarly, Katz et al. (2015) have shown that *Aulacoseira* blooms have historically been correlated not only with ice duration, but also with early and severe winters. Another factor in the success of *Aulacoseira* in spring may be related to radiatively-driven convective mixing under the ice in spring (Jewson et al., 2009), so changes to snow thickness or earlier disappearance of ice may have negative effects on *Aulacoseira* by reducing mixing strength under the ice. Unfortunately for *Aulacoseira*, the temperature dynamics of the lake changed during the last decades. For example, in 2014–2016, the ice-cover period in Southern Baikal lasted 76–99 days – starting later and ending earlier than in 1850–1990 (Shimaraev and Domysheva, 2013). This shortening of the ice cover period is caused by warmer winter conditions around Lake Baikal between 1896 and 2010, with air temperatures increasing by 1.9 °C in winter and 1.5 °C in spring over the last 100 years (Shimaraev and Domysheva, 2013). Hence, the lake freezes later and spring isothermal conditions start earlier than in the previous years (Shimaraev and Domysheva, 2013), the vegetation period of algae reduces and they sink faster out of the water column. This is unfavourable for growth of large diatoms because of their heavy filaments. Meanwhile, the unicellular diatom *Synedra* may be successful because its cells (formed by sexual reproduction in 2007–2016) are small, twisted and have no heavy silica valves, and thus do not sink so rapidly. We observed such *Synedra* cells in the water column round the year. This size difference may be one of the reasons why *Synedra* is becoming successful during the last 10 years and is replacing *Aulacoseira* as a dominant spring diatom (Bondarenko et al., 2017 in press). A recent paleolimnological study covering the last few decades (Roberts et al., 2018) supports our findings and also shows decreases in *Aulacoseira* and increases in *S. acus* remains in sediment cores. Other paleolimnological studies confirm that the Baikal diatom community is sensitive to climate. Studies spanning hundreds (Mackay et al., 1998), thousands (Bradbury et al., 1994), and hundreds of thousands of years (Khursevich et al., 2001) have shown fluctuations in abundance of *Aulacoseira* spp., *S. acus* and other diatom species in connection with climatic shifts.

Similar abundance decreases in large diatoms have occurred in many aquatic ecosystems. Paleolimnological data on diatoms from many lakes in the Northern Hemisphere show spatially coherent shift in diatom communities, with increases in planktonic *Cyclotella* species and decreases in heavily silicified *Aulacoseira* species (Rühland et al., 2008). Similar shifts have been observed in long-term monitoring data for Lake Tahoe (Winder et al., 2009) and the Laurentian Great Lakes (Reavie et al., 2017). These species replacements are most evident in regions where warming and increased length of the ice-free period have caused changes in light conditions and stratification patterns (e.g., Rühland et al., 2008; Winder et al., 2009; Reavie et al., 2017). While Baikal also shows recent declines in the abundance of *Aulacoseira* species (our data, Roberts et al., 2018), *Cyclotella* has not become more abundant as in other lakes, with *Synedra* becoming a new dominant. In the last century, *Cyclotella minuta* was the dominant autumn diatom in Baikal, with densities in the range of 150,000–200,000 cells/L in September-October (Popovskaya, 1987, 2000). On the other hand, *C. minuta* has played a relatively minor role in the spring plankton of the lake over that period (Kozhov, 1963; Popovskaya et al., 2015; Jewson et al., 2015). The abundance of *C. minuta* in spring 2016 was very low (215–260 cells/L), and it was not especially abundant in the autumn period of 2010–2016 either (maximum density of 14,800 cells/L). It is unclear whether the shift from *Aulacoseira* to *Synedra* dominance in Lake Baikal will persist in the future, and what its ecological consequences will be. The differences in cell size and silica demands

between these two species can potentially affect the cycle of elements in the lake, the export of organic material to the deep-water benthos and the movement of energy through the pelagic food web.

5. Conclusions

To assess recent ecological changes in Lake Baikal and provide a baseline for future comparisons, we sampled spring plankton communities from the pelagic zone of the lake in 2016 and compared these data with historical information. On the one hand, we found the appearance of small-sized cells of coloured and colourless flagellates, which are attributed to nutrient enrichment (e.g., Trifonova, 1990; Wehr and Sheath, 2003; Chekryzheva, 2008; Petrova et al., 2010) and increased dominance of small-sized species. On the other hand, we also detected a shift in the composition of cryophilic diatoms likely caused by warming, which worsens the conditions for previously dominant heavily silicified diatoms such as Aulacoseira baicalensis, A. islandica, and Stephanodiscus meyeri. The dominant role of this typical set of Baikal algal representatives has decreased and since 2007 S. acus, a smaller and weakly silicified diatom, has intensely developed annually in the spring plankton. As a result, the high spring phytoplankton biomasses that occurred every 3 to 4 years in the 1990s have not occurred recently and appear to have been replaced by low and consistent concentrations of between 500 and 1000 mg/m^3. The permanence and consequences of these changes for the food web are still unclear. It is also difficult to predict the future trajectory of the ecosystem, as warming continues to interact with increasing nutrient inputs, making it important to continue detailed monitoring of Lake Baikal.

Acknowledgments

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